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PROGENESIS AS A MEANS OF ABBREVIATING LIFE HISTORIES IN TWO NEW ZEALAND TREMATODES, *COITOCAECUM PARVUM* CROWCROFT, 1945 AND *STEGODEXAMENE ANGUILLAE* MACFARLANE, 1951.

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ABSTRACT

Metacercariae of *Coitocaecum parvum*, Crowcroft, 1945 and *Stegodexamene anguillae*, MacFarlane, 1951 encyst in their second intermediate hosts (crustaceans and fish respectively) in freshwater habitats in Canterbury. While encysted some metacercariae become sexually mature and produce eggs. Eggs from metacercariae of both species are viable and release miracidia capable of infecting the first intermediate snail host, *Potamopyrgus antipodarum* Gray, 1843. *Coitocaecum parvum* metacercariae are found to readily excyst on death of the crustacean host *Tenagomysis chiltoni* Tattersall, 1923. Excystation is considered a mechanism that aids in the dispersion of eggs from progenetic metacercariae.

Abbreviation of the life histories of these trematodes through progenesis is discussed.

KEYWORDS: *Coitocaecum parvum, Stegodexamene anguillae,* progenesis, trematodes, parasites, life history.

INTRODUCTION

A review of the literature indicates that only a very few trematodes complete their life histories entirely in freshwater habitats in New Zealand. Complete or partial life histories are known for only four species, Coitocaecum parvum Crowcroft, 1945 (= C. anaspidis Hickman, 1934 sensu MacFarlane, 1939; Holton, 1984);

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Telogaster opisthorchis MacFarlane, 1945; Stegodexamene anguillae MacFarlane,1951 and Deretrema minutum Manter,1954 (see Holton, 1983b). Each species utilises up to three hosts in its life history. Adult worms are parasites of a variety of freshwater fishes. Sporocysts and cercariae occur in the snail Potamopyrgus antipodarum Gray,1843 (host unknown for Deretrema). Metacercariae occur in either mysids and/or amphipods (Coitocaecum and Deretrema or bullies and inanga (Telogaster and Stegodexamene). In all these trematode species encysted metacercariae may undergo considerable growth and development, to such an extent that in Coitocaecum, Stegodexamene and Deretrema (fig 1a,1b,1c), well developed eggs are released into the cyst cavity. The proportion of metacercariae exhibiting progenesis may be as high as 8.5% for C.parvum and 47% for D.minutum (Holton, 1983a; Holton, 1983b). A figure is not available for S.anguillae.

Progenesis has been defined by Gould (1977, p485) as "paedomorphosis, produced by precocious sexual maturation of an organism still in a morphological juvenile state". The first report of progenesis in trematodes was by von Siebold (1835, cited by Stunkard,1959) who observed ovigerous metacercariae in the crayfish Astacus astacus. Since then many authors have speculated on the importance of progenesis in the life histories of trematodes (Grabda-Kazubska, 1976). It is often considered that abbreviation of the life history (from three to two hosts, by-passing the usual definitive host) can follow as a consequence of egg production by metacercariae (e.g; McMullen,1938; Deblock, 1977; Font,1980). However, this assumes a) that eggs are viable and b) that they are readily released from the metacercarial cyst and dispersed on death of the second intermediate host. Few workers have examined these assumptions experimentally. Successful infections of molluscs by miracidia from progenetic metacercariae have been achieved by Buttner (1950,1951), Bayanov (1975), Wootton (1957) and Stunkard (1959). However,in some species, eggs produced by metacercariae are not viable (Ameel,1937; Cheng,1957; Winstead and Couch,1981), and are incapable of infecting the first intermediate host. There have been no previous experimental studies of dispersal of eggs from progenetic metacercariae encysted in intermediate hosts.

In this paper abbreviation of the life histories of two New Zealand trematodes is demonstrated experimentally. Excystation of C.parvum metacercariae is also examined and discussed as a method of dispering eggs trapped within cysts of progenetic metacercariae.

METHODS

Mysid (Tenagomysis chiltoni Tattersall,1923) and amphipod (Paracalliope fluviatilis (Thomson,1879)) hosts of C.parvum and fish hosts (Gobiomorphus cotidianus McDowall,1975) of Stegodexamene anguillae were collected with a hand-net from the Selwyn River, Lake Ellesmere (43° 44'S,172°26' E; N.Z.M.S.1,S83,706388).

INFECTION EXPERIMENTS

Mysids, amphipods and fish were decapitated, their tissues teased into saline (0.75% NaCl in distilled water) and examined for metacercariae. Three progenetic C.parvum metacercariae were collected from mysids, four from amphipods and two S.anguillae from fish.

To collect eggs for infection experiments, cysts were gently ruptured with a blunt-ended needle. Eggs collected from cysts of C.parvum from mysids and from amphipods were placed in two Petri dishes each containing twenty laboratory-bred Potamopyrgus antipodarum, Elodea and chalk fragments and maintained at room temperature (18-22 C). After two weeks snails were crushed and their tissues examined for sporocysts. (For methods used in obtaining parasite-free snails see Holton, 1983a).

Eggs from metacercariae of S.anguillae were also placed with twenty laboratory-bred snails,Elodea and chalk fragments and maintained at room temperature for four weeks. Sixty snails dissected as controls were not infected with parasites.

EXCYSTATION OF METACERCARIAE

Casual observations on C.parvum indicated that metacercariae encysted in T.chiltoni escape their cysts soon after death of this host. To examine this, twenty large mysids were decapitated and placed in groups of five in four Petri dishes containing saline. After thirty minutes the tissues of each mysid were teased apart and examined for excysted parasites.

A further sixty metacercariae were collected fresh from mysids and washed several times in saline. Thirty cysts were added to a watch glass containing five drops of fluid from the hepato-pancreas of mysids in 5mls distilled water. At fifteen minute intervals for two and a half hours the number of excysted metacercariae were counted. The remaining thirty cysts, used as controls, were kept in saline for twenty-four hours.

RESULTS

The results of snail infection experiments are presented in Table 1.

Infected laboratory-bred snails were recovered from all three Petri dishes after isolation with eggs from progenetic C.parvum and S.anguillae metacercariae.

None of the snails infected with C.parvum was shedding cercariae after two weeks. However, on dissection, sporocysts were found in the tissues of three of these snails. Sporocysts

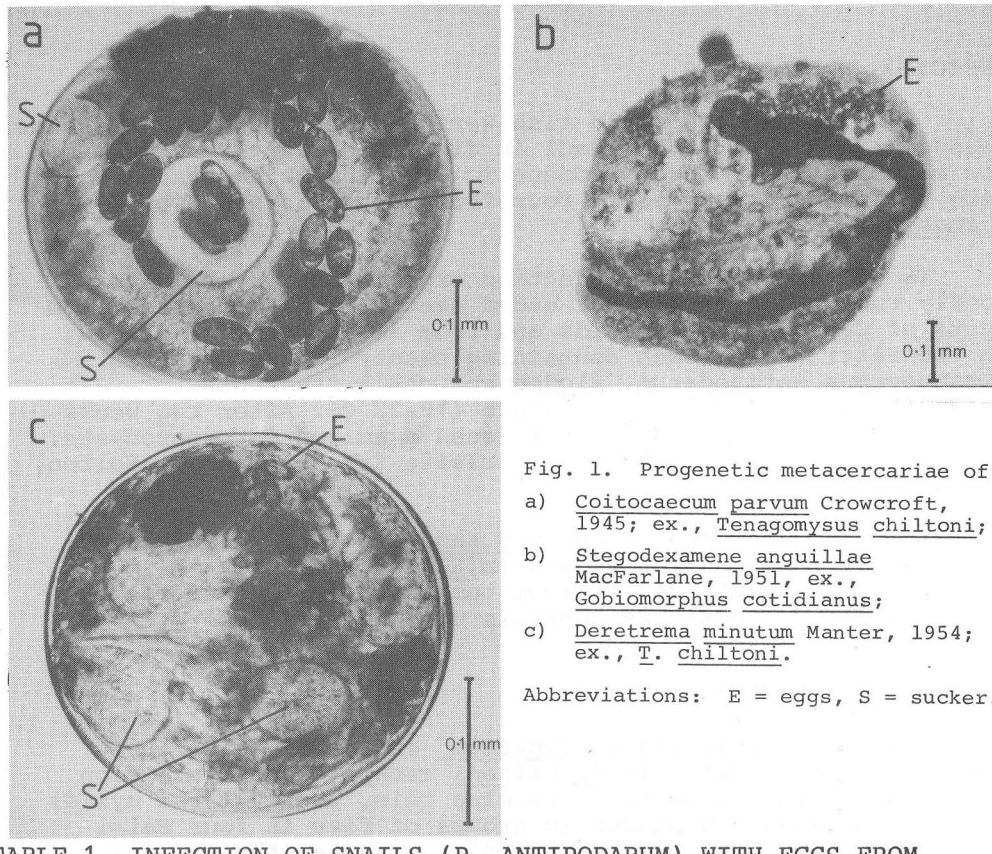

Fig. 1. Progenetic metacercariae of
a) Coitocaecum parvum Crowcroft, 1945; ex., Tenagomysus chiltoni;
b) Stegodexamene anguillae MacFarlane, 1951, ex., Gobiomorphus cotidianus;
c) Deretrema minutum Manter, 1954; ex., T. chiltoni.

Abbreviations: E = eggs, S = sucker.

TABLE 1. INFECTION OF SNAILS (P. ANTIPODARUM) WITH EGGS FROM PROGENETIC C. PARVULUM AND S. ANGUILLAE METACERCARIAE.

Parasite.	Source of Eggs	Number of snails.	Number Infected.	Percent Infected.
C.parvum	Mysids	20	1	5
C.parvum	Amphipods	20	2	10
S.anguillae	Bullies	20	1	5

were small (0.48 X 0.072mm) and evidently immature by comparison with sporocysts from naturally infected snails. (see Holton, 1983a).

Cercariae of Stegodexamene anguillae were found emerging from one snail four weeks after infection. (Identification of cercariae based on MacFarlane,1951).

A total of eighty three C.parvum metacercariae were collected from twenty mysids thirty minutes after death of the hosts. Of these, 82 (99 %) had excysted and were active. Eggs collected from progenetic metacercariae hatched after 2-16 days in distilled water.

The results of excystation experiments using fluid from the hepato-pancreas of the mysid host are presented in Table 2.

TABLE 2. EXCYSTATION OF C.PARVUM METACERCARIAE AFTER TREATMENT WITH HEPATO-PANCREAS FLUID FROM MYSIDS.

	Time in minutes									
	15	30	45	60	75	90	105	120	135	150
	Percent Excysted %									
Treated n=30	40	60	65	65	70	70	75	79	81	85
Control n=30	0	0	0	0	0	0	0	0	0	0

Eighty-five percent of metacercariae treated with hepato-pancreas fluid from mysids had excysted within two and one half hours. Excystation was most rapid during the first thirty minutes.

All thirty metacercariae used as controls were still encysted after 24 hours in saline. To ensure that these metacercariae were not dead they were transferred to a watch glass containing five drops of hepato-pancreas fluid in 5mls of distilled water. All but two metacercariae excysted within 30 minutes.

DISCUSSION

In this study, two of the factors upon which abbreviation of the life histories of progenetic trematodes may depend have been examined. These are firstly, the viability of eggs produced by metacercariae and secondly, the dispersion of eggs from within the confines of the cyst. Eggs from progenetic C.parvum and S.anguillae metacercariae were found to be viable and capable of infecting the snail host, P.antipodarum. In addition, C.parvum metacercariae, whether progenetic or not, were found to excyst readily on death of their mysid host and eggs released from the cyst hatched after a few days in water.Although there are many reports from the literature on experimental excystation of metacercariae, most of these involve treating metacercariae with enzymes from warm-blooded definitive hosts. Excystation of a metacercariae under the influence of an intermediate crustacean host's enzymes has not been previously

documented. Even though such metacercariae will eventually die, excystation under these conditions allows for the dispersion of eggs and continuation of the life history. Excystation of S.anguillae metacercariae has not been examined.

Progenesis appears to a common phenomemon among New Zealand trematodes inhabiting freshwater animals. Three of the four species maturing in freshwater fishes and for which life histories are at least partly known, exhibit progenesis. It is tempting to speculate why progenesis is common in New Zealand trematodes. Two factors are considered. These are the apparent instability of New Zealand freshwater habitats and the life history patterns of the definitive hosts.

New Zealand streams are generally considered to provide unpredictable habitats for stream organisms (Winterbourn et al,1981; Winterbourn,1982). Many streams, especially in the South Island, flow over extensive gravel beds which may be dry in summer but liable to heavy, temporally variable floods in winter. Intermediate hosts may, under these conditions, become stranded in marginal pools where mortality is high and where no final hosts are available for completion of the parasite life history. In addition, almost all of the fish hosts utilised by C.parvum and/or S.anguillae (eels, inanga, bullies and smelt) may spend a considerable portion of their life histories at sea (Burnet,1969; McDowall,1978). Marked seasonal migrations are common in many of these fishes.

Perhaps as a consequence of these two factors the definitive hosts of the trematodes under discussion may, periodically, be unavailable for completion of the life history. Egg production by metacercariae, under these conditions, provides an insurance against termination of the life history by permitting the life cycle to "tick over" in the absence of the fish definitive host.

Parasites, perhaps more than any other groups of organisms, face considerable odds against the successful completion of their life histories (Schmidt and Roberts, 1977). This is especially so for trematodes which are dependent on minute, short-lived, free-swimming larval stages which have only a few hours to locate and infect a suitable host. The odds against the parents producing surviving offspring are overcome, to some extent, by the evolution of mechanisms that increase the rate of reproduction, reduce risks and ensure a return on reproductive investment (Schmidt and Roberts, 1977; Clark,1978). Progenesis serves all of these functions. The parent trematode benefits not only by eliminating some of the risks involved in transferring its metacercaria to a suitable definitive host, but also by increasing the number of its offspring in the population with the potential to reproduce. In addition to these advantages Progenesis also allows for the completion of the life history in the absence of suitable definitive hosts. It is a mechanism that adds considerable flexibility to the life histories of trematodes (Clark,1974).

The relatively small proportion of C.parvum metacercariae which achieve progenesis suggests, in this species at least, that there may also be some disadvantages in by-passing the definitive host. Progenetic metacercariae are presumed to reproduce by self-fertilization since the cyst wall acts as a barrier to copulation. In the long term at least, this may lead to homozygosity and perhaps reduce the capability of the parasite to leave descendents in changing environmental conditions (Grabda-Kazubska,1976; Font,1980). Retention of the definitive host in the life history under these conditions allows for cross-fertilisation and genetic exchange between individuals to occur.

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